

# LESQUERIA: AN EARLY ANGIOSPERM FRUITING AXIS FROM THE MID-CRETACEOUS<sup>1</sup>

PETER R. CRANE<sup>2</sup> AND DAVID L. DILCHER<sup>3</sup>

## ABSTRACT

*Lesqueria elocata* (Lesq.) Crane & Dilcher, an early angiosperm fruiting axis, is described from the mid-Cretaceous (Upper Albian–Middle Cenomanian) Dakota Formation of central Kansas and the Woodbine Formation of northeastern Texas. The species is based on three-dimensional molds preserved in sandstone. The fruits (multifollicles) comprise 175–250 follicles borne helically, in a tight, more or less spherical or ovoid head. The receptacle below the gynoecium is cylindrical, elongated, and bears numerous, helically arranged, persistent laminar flaps. The bases of these flaps are diamond-shaped at their attachment to the receptacle, but it is not known whether they are stamens or perianth parts. The follicles are short stalked, with two terminal prolongations, and dehiscent along a single adaxial suture. The follicles contained 10–20 seeds arranged in two longitudinal rows. The former assignment of *L. elocata* to *Williamsonia* (Bennettitales) is rejected and *Lesqueria* is shown to be most similar to Recent magnoliid angiosperms. *Lesqueria* is one of a diverse group of extinct mid-Cretaceous magnoliid flowering plants.

Until recently, knowledge of early angiosperms has been almost exclusively restricted to isolated pollen grains and leaves. Although some conclusions may be drawn about the systematic relationships of the plants from which these organs were derived, progress in interpreting the systematic affinities of the earliest flowering plants has been considerably inhibited by a lack of knowledge of their reproductive structures. In this paper we describe an early angiosperm fruit from the mid-Cretaceous of central United States. The fruit (multifollicle) comprises a receptacle with a terminal cluster of tightly packed follicles. We discuss its systematic relationships and briefly evaluate its evolutionary significance in relation to the known fossil record of early angiosperm reproductive structures.

One element in the early formulation of magnoliid floral theory was the superficial similarity of generalized *Magnolia*-like flowers to the 'flowers' of the Bennettitales (Arber & Parkin, 1907). Although it is now clear that these two kinds of reproductive organs are very different in detailed structure, their superficial similarity creates some

difficulties for the determination of imperfectly known fossil material. In his review of the bennettitalean genus *Williamsonia*, Seward (1917) excluded several species, including *W. elocata* Lesq. from the Dakota Sandstone Flora of Kansas. Wieland (1928) described a species similar to *W. elocata* from the same flora as *W. hespera* and also expressed doubt as to its relationship with *Williamsonia*. In this paper we reinterpret both of these species based on five specimens from the Dakota Sandstone Flora, including the type material of *W. hespera*, and two specimens from the Woodbine Formation of Texas. Both are interpreted as angiosperm fruits and united as a single species *Lesqueria elocata* (Lesq.) Crane & Dilcher.

## MATERIAL

The seven specimens described in this paper are preserved as three-dimensional molds in sandstone. Five are from the classic Dakota Sandstone Flora of Kansas, the other two are from the Woodbine Formation of Texas.

Almost all of the large plant fossil collections

<sup>1</sup> We would like to thank C. P. Daghljan, E. M. Friis, G. J. Gastony, T. M. Harris, W. Kovach, K. Longstreth, and F. Potter for their advice and assistance at various stages of this work; R. Baxter, University of Kansas, H. Becker and P. Richardson, New York Botanical Garden, C. McGregor, Geological Survey of Canada, V. Hamilton and B. Tiffney, Yale University, F. Hueber, United States National Museum, and the Field Museum of Natural History, for the loan of specimens; and M. Rohn and P. Quasthoff for drawing the reconstructions. This research was supported by NSF grant DEB 77-04846 to D. L. Dilcher. Travel funds provided for P. R. Crane during the early part of the study by the British Council and Reading University Research Board are gratefully acknowledged.

<sup>2</sup> Department of Geology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.

<sup>3</sup> Department of Biology, Indiana University, Bloomington, Indiana 47405.



from the Dakota Sandstone (Dakota Formation) are preserved as impressions or molds in a fine- to medium-grained ferruginous sandstone. Although we have seen similarly preserved material in situ in sandstones at various central Kansas localities, the specimens considered here are from the collections of the University of Kansas at Lawrence (UKDSC), the Field Museum of Natural History, Chicago (FM-P), the Peabody Museum of Natural History, Yale University, New Haven (PMNH), and the United States National Museum (USNM). Large collections of the 'Dakota Sandstone Flora' were assembled by Sternberg and others in the mid-nineteenth century (see Andrews, 1980) principally from surface weathered sandstone blocks in Ellsworth County. The locality for these specimens is often simply given as Ellsworth County, with no further details. Brief descriptions and discussions of the Dakota Sandstone Flora are given by Meek and Hayden (1858), Newberry (1859, 1860a, 1860b), Heer (1861), Marcou (1864), Capellini and Heer (1867), Bartsch (1896), Gould (1900a, 1900b, 1901), Berry (1920), Tester (1931), and Baxter (1954). More extensive reports and illustrations were given by Lesquereux (1868, 1874, 1878, 1883, 1892), Newberry (1868), and Gress (1922). The flora is dominated by angiosperm leaves and over 400 species have been described (Lesquereux, 1892).

Despite considerable lateral sedimentological variation, the Dakota Formation in Kansas is generally divided into two members, neither of which constitute mappable units (Franks, 1975); the Terra Cotta Clay Member below and the Janssen Clay Member above (Plummer & Romary, 1942). Sandstones occur throughout both members but the classic Dakota Sandstone Flora is probably principally from the sandstone facies of the Janssen Clay Member. The age of the Dakota Formation in Kansas is firmly bracketed as no older than late Albian (Scott, 1970a, 1970b; Ward, 1981) and no younger than Cenomanian (Hattin, 1965, 1967; Eicher, 1975). It seems likely that the Dakota Formation in this area straddles the Upper and Lower Cretaceous boundary (Zeller, 1968; Kauffman et al., 1976).

Two specimens of *L. elocata* are known from the Woodbine Formation (Woodbine Sand) of northeast Texas. One was kindly donated by Ms. V. Hamilton (IU 15726-4419); and the other (USNM 326817) was identified by Brown (1958: 359) as *Isoetites* sp. Fossil plants from the Woodbine Formation have been described by Knowl-

ton (1901), Berry (1912, 1917, 1922), Winton (1925), and MacNeal (1958). The flora is dominated by angiosperms, and over 80 species of leaves and other organs have been recognized (MacNeal, 1958). The Woodbine Formation comprises diverse sediments divided into four members, from the base upward; the Dexter Member, the Eules Member (more or less laterally equivalent to the Red Branch Member), the Lewisville Member, and the Templeton Member. The Templeton, Lewisville, and Eules Members are predominantly marine in origin, whereas the Red Branch and Dexter Members are predominantly non-marine sands, clays, and carbonaceous shales. Most of the plants, and probably our specimens, are from the Red Branch or Dexter Members. Although there are some plant species unique to the Woodbine Formation, the flora is very similar to the typical 'Dakota Sandstone Flora' of Kansas and Nebraska (MacNeal, 1958). Marine and brackish water invertebrates from the upper part of the Janssen Clay Member suggest a correlation with the Woodbine Formation in northeast Texas (Hattin, 1965). The age of the Woodbine Formation is generally regarded as Cenomanian (Stephenson, 1952; Hedlund, 1966; Pessagno, 1969). All of the material described in this paper, therefore, comes from sediments of similar age, probably equivalent to zone III, of the palynological zonation established by Brenner (1963), Doyle (1969), Doyle and Robbins (1977), and others for the mid-Cretaceous of the Atlantic Coastal Plain.

#### SYSTEMATICS

The measurements given in the description are based on all seven specimens, with ranges and common dimensions given whenever possible.

***Lesqueria* Crane & Dilcher, gen. nov. TYPE: *Lesqueria elocata* (Lesq.) Crane & Dilcher.**

**DIAGNOSIS:** Fruit consisting of a receptacle bearing a tight, ovoid, cluster of follicles at the apex, and other floral organs below. Receptacle stout, elongated, consisting of a distal, swollen, ovoid, gynoecial zone bearing follicles; with an elongated, more or less cylindrical zone below, bearing numerous helically arranged laminar flaps. Bases of the flaps diamond-shaped, forming a distinctive pattern on the receptacle. Base of flower delimited by a narrow transverse ridge. Follicles narrowly ellipsoidal with a distinct



adaxial suture; very short stalked and with elongated bifid tips.

DERIVATION: After Leo Lesquereux who originally described the type species.

***Lesqueria elocata* (Lesq.) Crane & Dilcher, comb. nov.** NEOTYPE: UKDSC 203—Ellsworth County, Kansas.

DIAGNOSIS: As for the genus.

SYNONYMS: *Williamsonia elocata* Lesq.

*Williamsonia* (?) *hespera* Wieland.

REFERENCES: *Williamsonia elocata* Lesquereux (1892: 89, pl. 2, figs. 9, 9a) (brief description, discussion, and line drawings).

*Williamsonia elocata* Lesq. (Wieland, 1928: 39–41, fig. 5) (discussion and line drawing).

*Williamsonia* (?) *hespera* Wieland (1928: 41–47, figs. 7–10) (description, discussion, and photographs).

*Williamsonia elongata* Lesq. (Seward, 1917: 462) (rejects the assignment to *Williamsonia*; orthographic error).

*Isoetites* sp. (Brown, 1958: 359) (brief mention).

OTHER MATERIAL: PMNH 2403–2405, Dakota Formation, Kansas; FM-P3056, Dakota Formation, Ellsworth County, Kansas; USNM 2782, Dakota Sandstone, Fort Harker, Kansas; USNM 50598, Dakota Formation, Ellsworth County, Kansas; USNM 326817, Woodbine Formation, 5 miles SE of Dexter, Texas; IU 15726-4419, Woodbine Formation, Denton County, Texas.

NUMBER OF SPECIMENS EXAMINED: 7.

FIGURES: 1–32, 42A–G, 47.

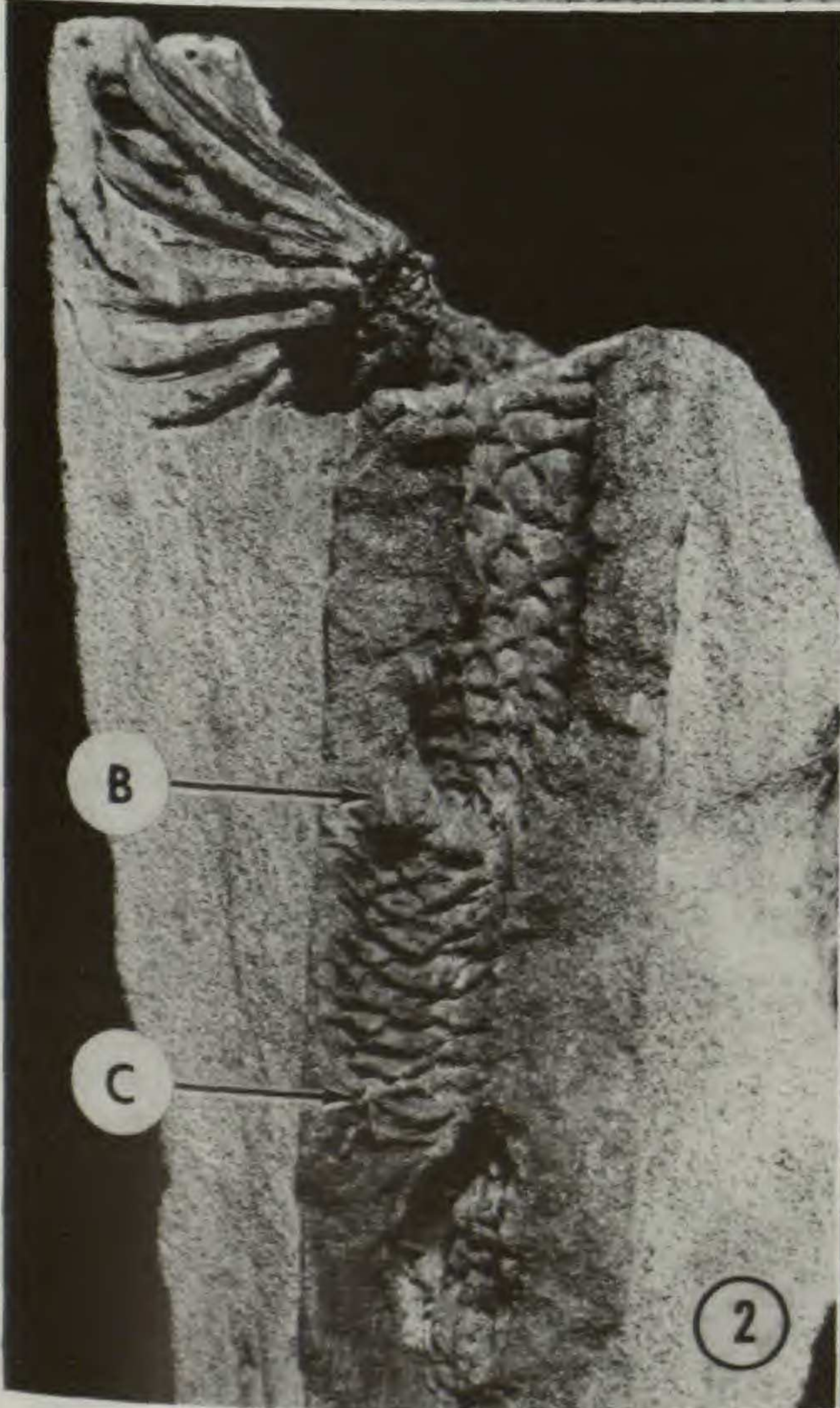
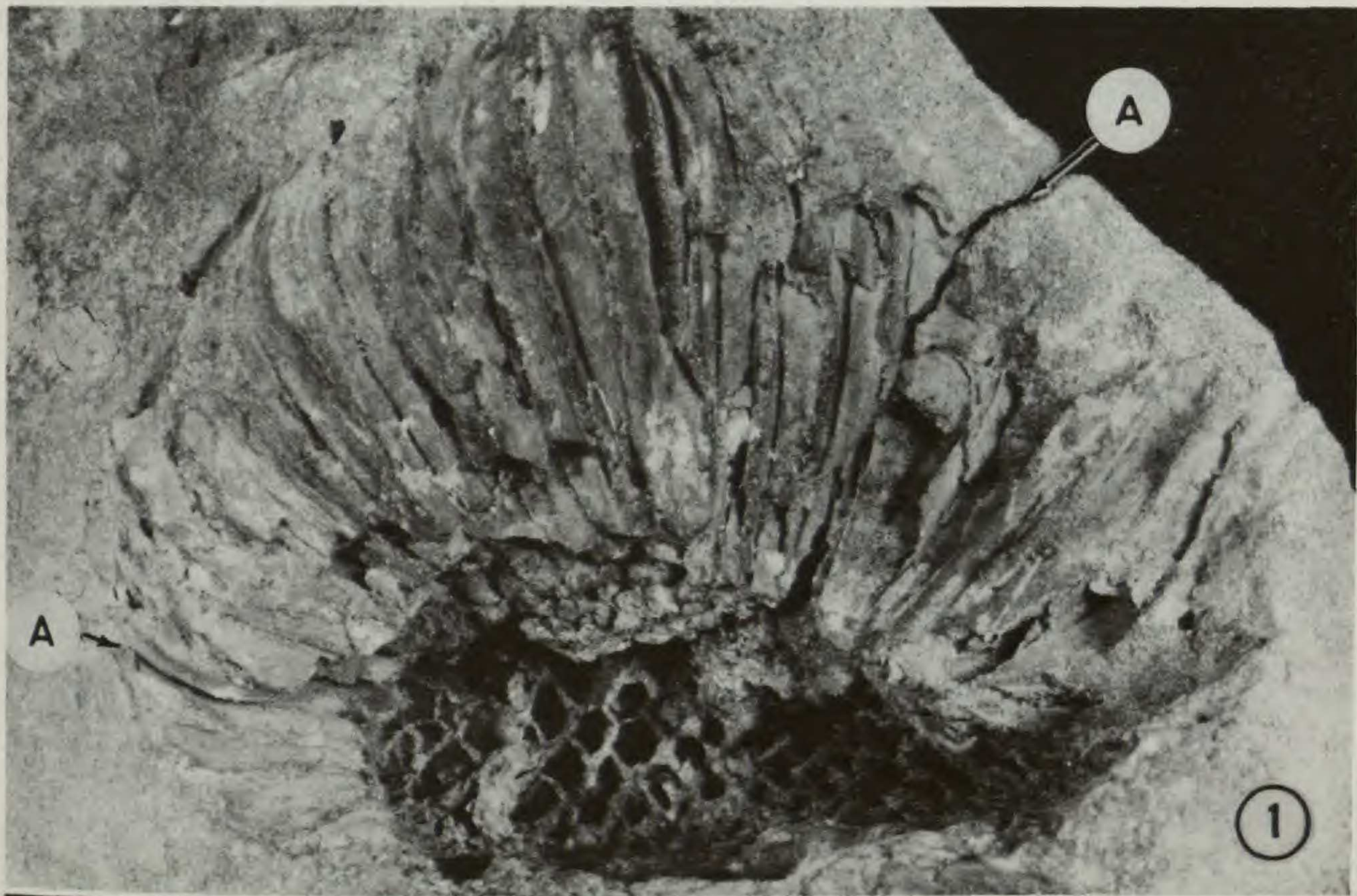
DESCRIPTION: Fruit borne at the apex of a stout vegetative axis, ca. 10 mm diam., which also shows the bases, or former attachment, of 4 other fruits. Surface of axis with a few transverse grooves and ridges immediately below the re-

FIGURES 1–3. *Lesqueria elocata* Crane & Dilcher, comb. nov., UKDSC 203, Dakota Sandstone, central Kansas.—1. Ovoid head of clustered, narrowly elliptical, follicles prior to fracturing, A–A indicates plane of fracture; bases of follicles and their attachment to the receptacle missing;  $\times 2.5$ .—2. Longitudinal fracture of a three-dimensional mold, showing curved follicles borne on the terminal, swollen, gynoeical zone of a long receptacle. Below the gynoeical zone note: the bases of the numerous helically arranged flaps and the penetration of sandstone matrix approximately midway along the cylindrical portion of the receptacle (B), the constriction at the receptacle base and point of attachment to the vegetative branch (C);  $\times 1.5$ .—3. Counterpart of Figure 2, note the attachment of the receptacle to the vegetative branch and the bases of other receptacles projecting into the sediment, see Figure 8 for details;  $\times 1.5$ .

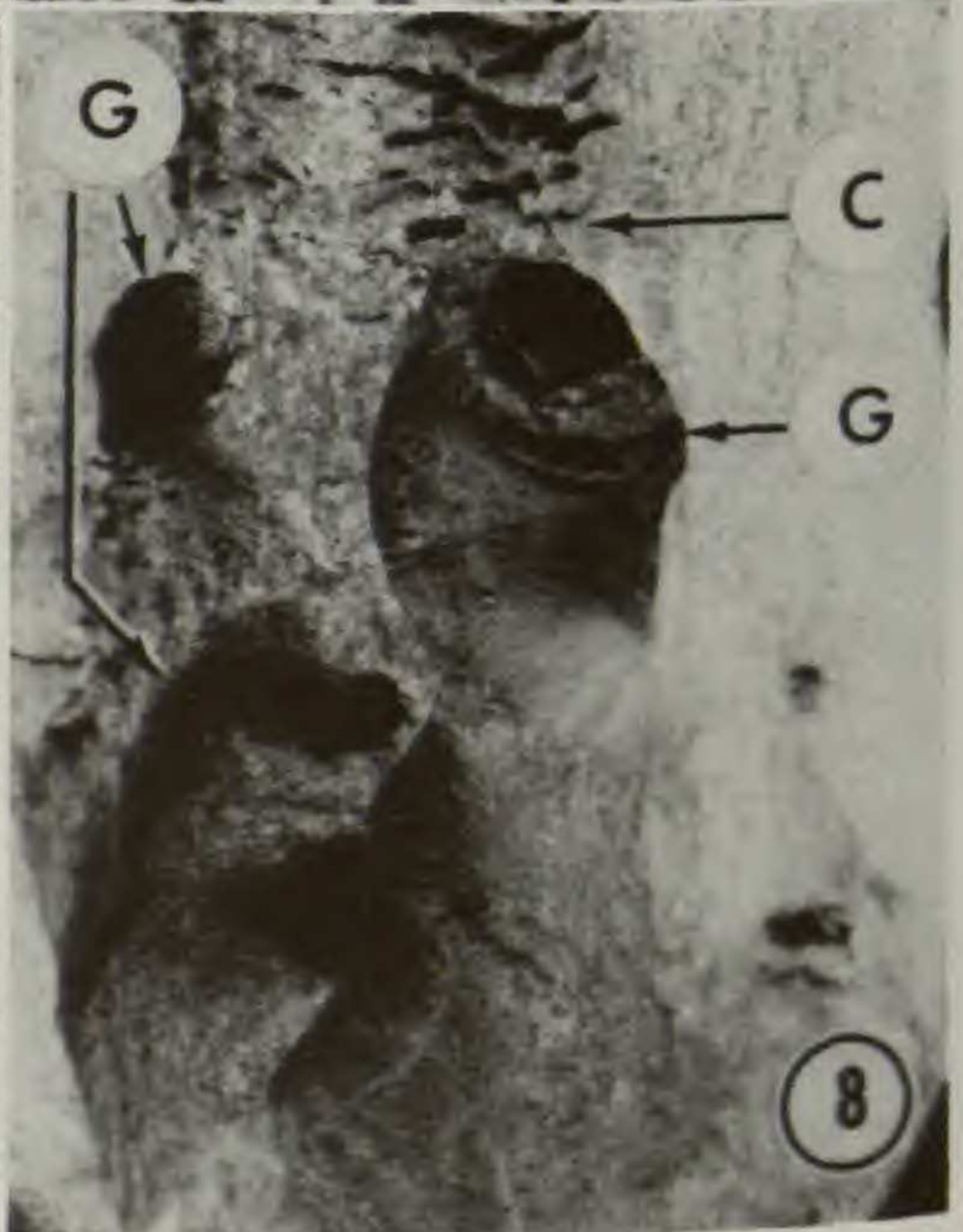
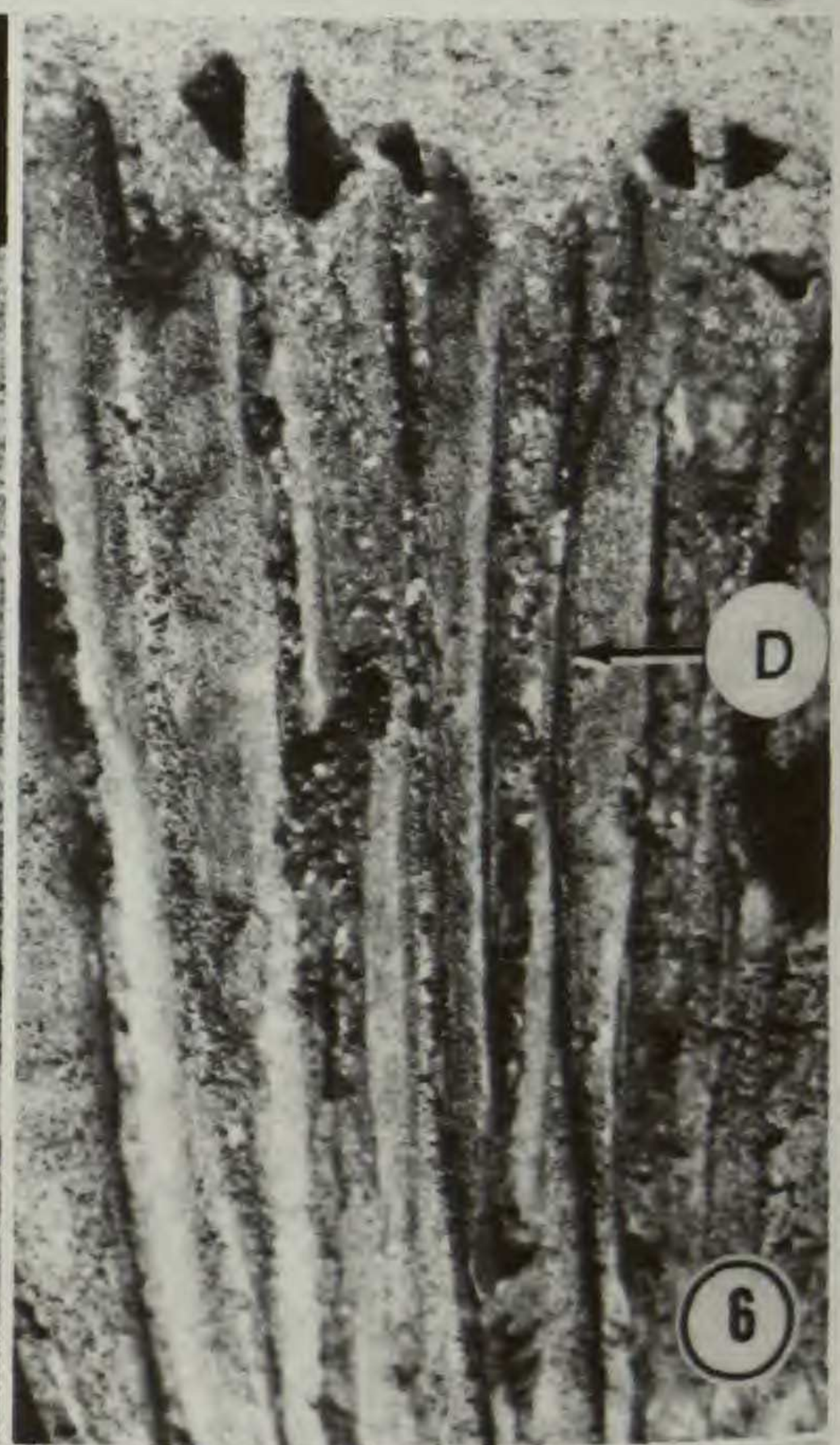
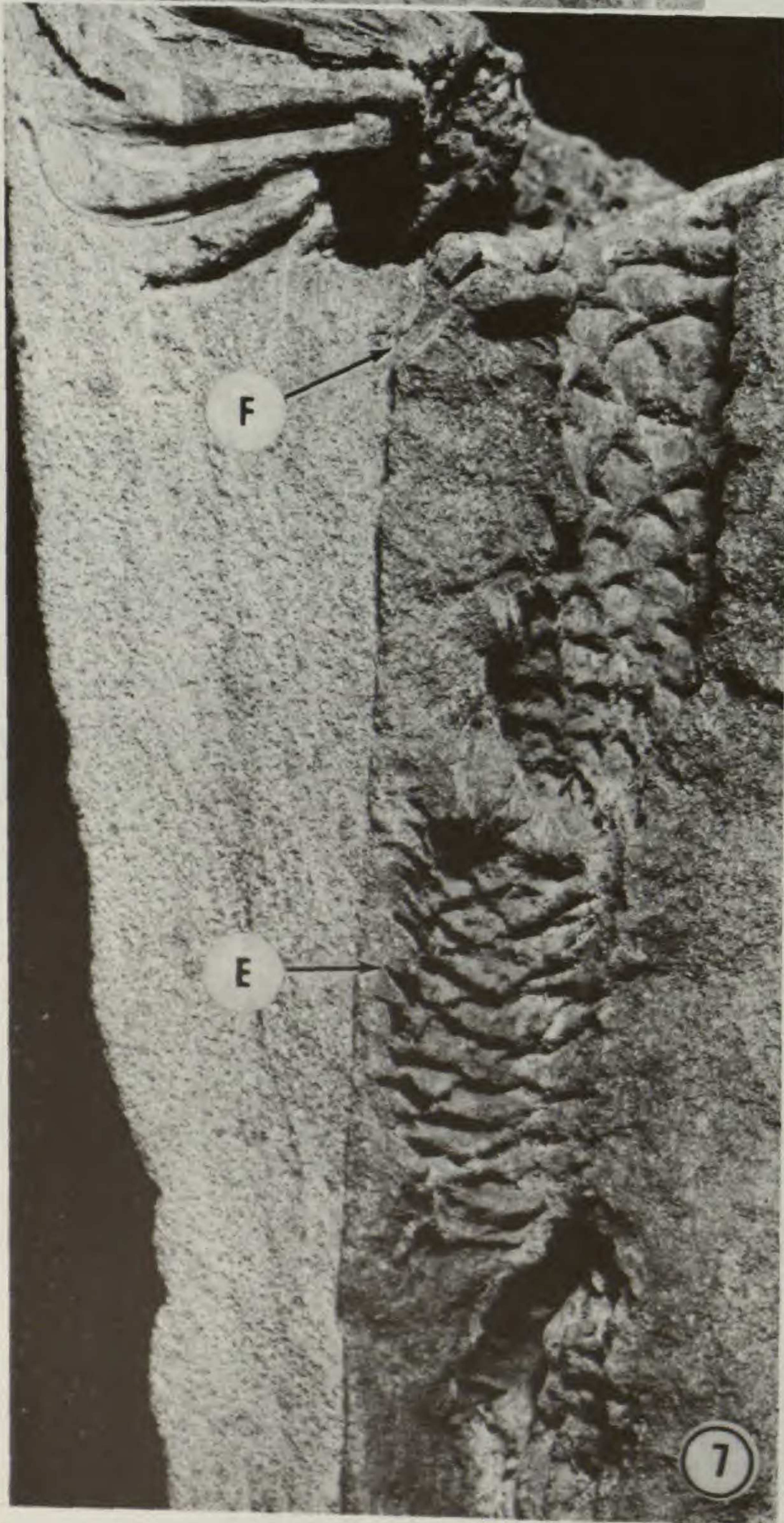
FIGURES 4–8. *Lesqueria elocata* Crane & Dilcher, comb. nov., UKDSC 203, Dakota Sandstone, central Kansas.—4. Ovoid head of follicles seen obliquely from above after the transverse fracture along A–A (Fig. 1) but before longitudinal fracture. Note the diamond-shaped bases of the flaps on the upper part of the cylindrical receptacle, and the molds of individual follicles;  $\times 1$ .—5. Counterpart of transverse fracture in Figure 4 seen from below, showing molds and locule casts of individual follicles;  $\times 1$ .—6. Detail of transverse fracture plane in Figure 4, showing paired, triangular cavities caused by the curved, double follicle tips. Note the lower parts of two follicle molds showing the groove (D) caused by the abaxial follicle surface which diverges at the apex into the two follicle tips;  $\times 5$ .—7. Detail of longitudinal fracture in Figure 2 showing the gradual change in the shape of the flap bases along the cylindrical receptacle. Note the short flaps (E) toward the base of the receptacle; at the apex the longest flaps (F) form a collar around the base of the head of follicles;  $\times 2.5$ .—8. Composite photograph, from different orientations of the specimen in Figure 3 showing (C) the base of the receptacle and (G) the bases or attachment points of three other receptacles;  $\times 2$ .

FIGURES 9–14. *Lesqueria elocata* Crane & Dilcher, comb. nov., UKDSC 203, Dakota Sandstone, central Kansas.—9. Detail of transverse fracture plane in Figure 5 (A–A, Fig. 1) showing several follicles seen from below. Note the variable extent to which sediment has penetrated the follicles both adaxially and apically to form the locule casts, and therefore the extent to which internal and external features of the follicles can be interpreted from the specimen. The paired triangular cavities are formed by the upcurved double tips of follicles attached lower down on the receptacle;  $\times 5$ .—10. Part of Figure 9 in different orientation showing cavities in a locule cast interpreted as those of seeds (H);  $\times 5$ .—11. Part of Figure 9 in different orientation showing the outline of a seed in the locule cast formed by the distorted fruit wall (I), and the fine double groove formed by the two external adaxial ridges on the follicles (J);  $\times 5$ .—12. Detail of part of Figure 9 showing the impressions of the two adaxial ridges;  $\times 30$ .—13. Detail of part of the specimen in Figure 9 seen obliquely from below and showing the grooves (J) left by the adaxial ridges of the follicles, and penetration of sediment through the adaxial suture;  $\times 5$ .—14. Detail of part of Figure 1 showing sections of the cavities left by follicles. Note in each follicle the impressions of two adaxial ridges which comprise the adaxial crest, one abaxial ridge, and two lateral ridges;  $\times 4$ .

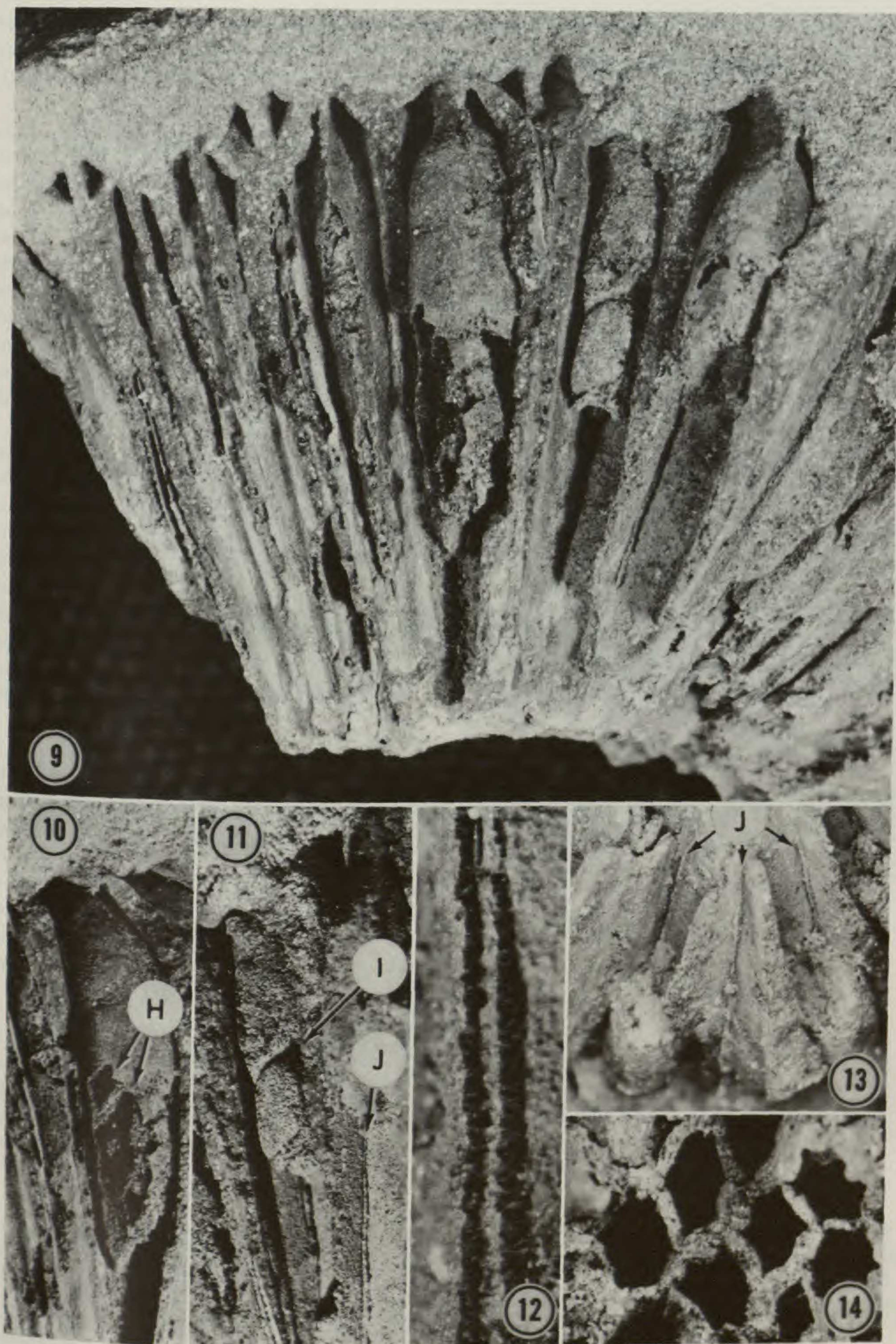




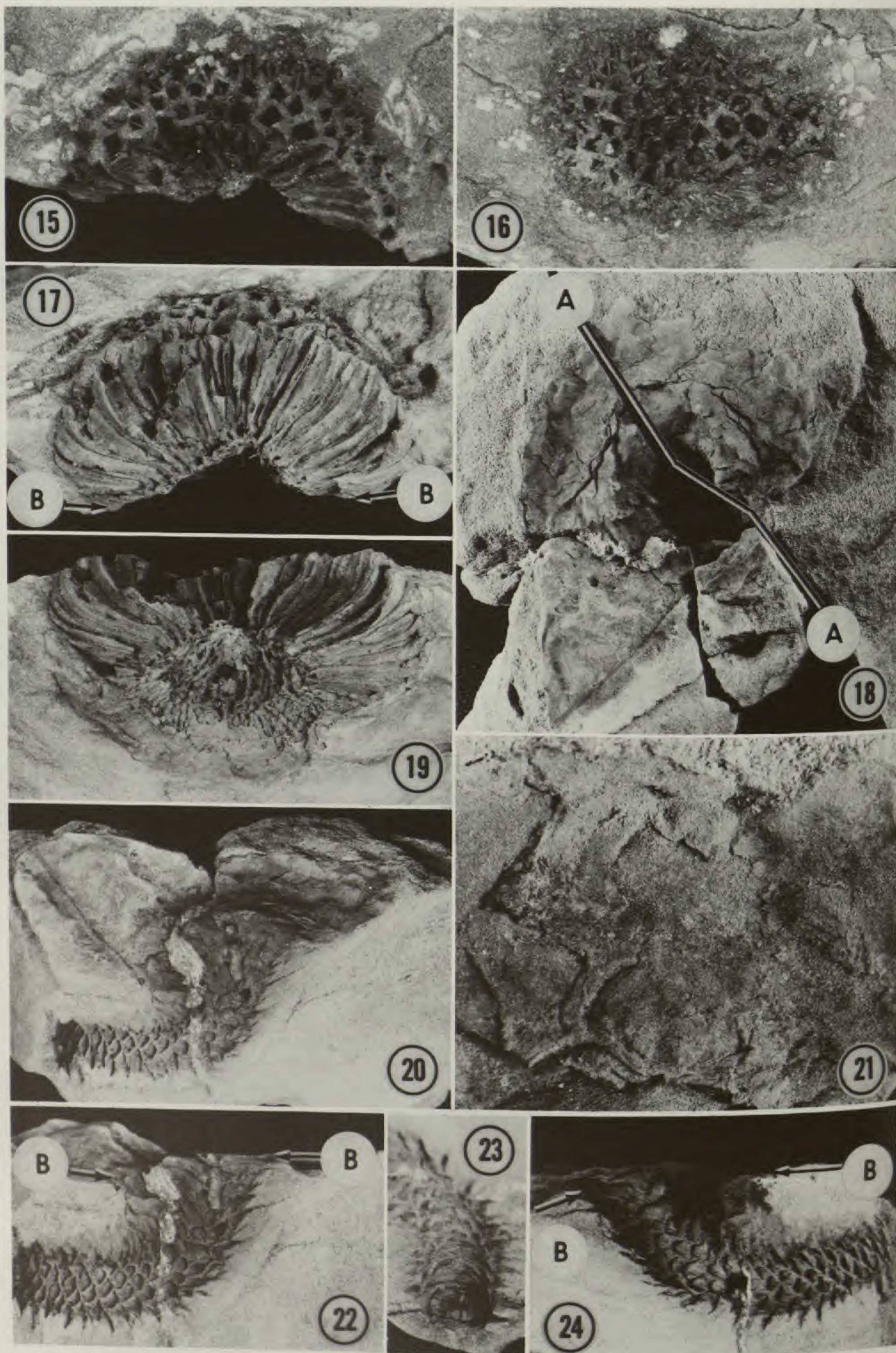












FIGURES 15-24. *Lesqueria elocata* Crane & Dilcher, comb. nov., Dakota Sandstone, central Kansas.—15. PMNH 2403, transverse fracture of a head of follicles seen from above, showing cavities left by follicles and the paired cavities formed by the double follicle tips;  $\times 1$ .—16. FM-P3056, transverse fracture through a head of curved follicles: notice that the fractures become increasingly tangential toward the circumference of the head;



ceptacle, otherwise more or less smooth. Maximum length of vegetative axis preserved, 28 mm. Total length of longest specimen seen, 88 mm.

Receptacle stout, elongated, to 56 mm long; comprising a distal, swollen, ovoid, gynoecial zone bearing follicles, with an elongated more or less cylindrical zone below. Gynoecial zone of receptacle to 14 mm long, to 25 mm diam. (maximum), bearing ca. 175–250 follicles tightly packed into a more or less spherical or ovoid head, ca. 37–65 mm diam., and to 35 mm high. Follicles borne helically, diamond-shaped in section at their attachment to the receptacle. Gynoecial zone abruptly or gradually tapered into the apex of the cylindrical zone below.

Receptacle below the gynoecial zone 40–42 mm long, ca. 8 mm diam., broadening slightly where it joins the gynoecial zone and bearing 110–150 helically arranged laminar flaps which have distinctive diamond-shaped bases where they are attached to the receptacle. Diamond-shaped bases 2–4 mm high, 2–4.5 mm wide distally; generally about as wide as high, occasionally higher than wide; gradually becoming shorter and wider toward the base where they are 1.5–3 mm high, 3.5–6 mm wide.

Distal flaps expanded at their apex into a prominent lamina to 20 mm long, and to 17 mm wide (largest flap incomplete in length and width), occasionally with a weak adaxial keel. Proximal flaps short, to 2 mm long (always incomplete). Upper flaps crowded and imbricate, forming a persistent irregular collar below the gynoecial zone. Lamina surface with a fine granular texture, showing no obvious venation or other morphological features.

Base of receptacle constricted where it joins

the vegetative axis and with a narrow transverse ridge below. Base of receptacle showing a central pith surrounded by 10 xylem wedges. Xylem cylinder surrounded by softer tissue.

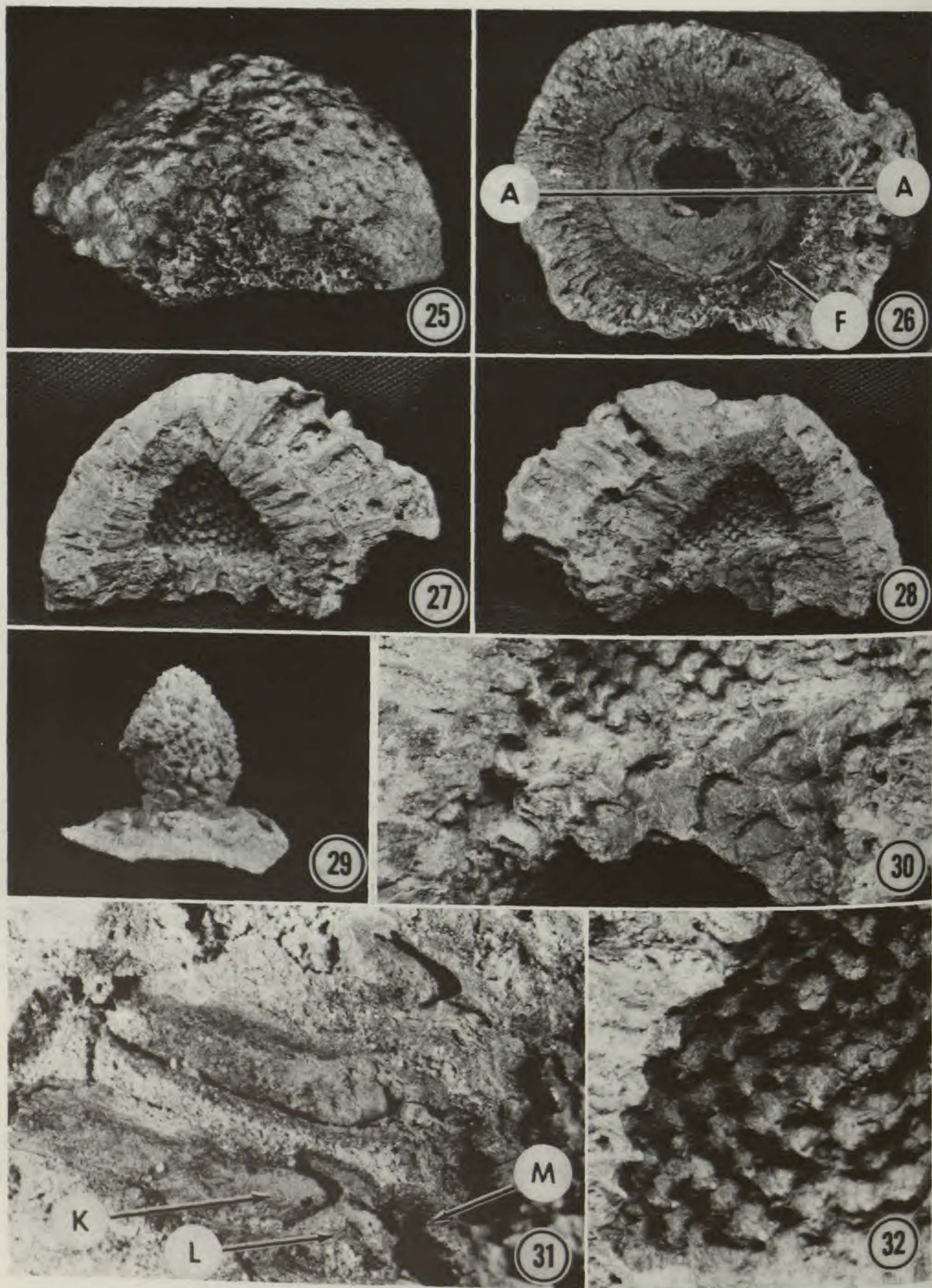
Follicles narrowly ellipsoidal, more or less straight or with strong upward curvature in the distal third, particularly toward the base of the follicle cluster. Individual follicles 9–24 mm long, 1.5–4 mm wide. Follicles contracted just above the attachment to the receptacle into a very short stalk-like constriction 2 mm long, and extended apically into an elongated bifid tip. Stalk 1 mm wide at its midpoint, broadening proximally to a diamond-shaped attachment to the receptacle, 1–2 mm high, 1–2 mm wide. Follicles with two narrow terminal prolongations 3–5 mm long forming a distinct bifid tip. Each prolongation triangular in cross section, ca. 0.5–1 mm thick (maximum); the inner surface of each pair parallel, and ca. 0.5 mm apart. Follicles attached to the receptacle at high angles of ca. 70–90°.

Follicles with a median, longitudinal, adaxial suture along the entire length, flanked on either side by a low ridge ca. 0.2 mm high, and 0.2 mm broad, forming an adaxial crest. Follicles dehiscing adaxially from the distal end along the suture; also splitting apically between the 2 prolongations. Follicles diamond-shaped in transverse section, to 4 mm high, slightly higher than broad. Abaxial follicle surface generally featureless externally or with a single ridge, frequently with a weak median groove internally. Lateral margins with a prominent ridge in their median part; ridge less conspicuous toward the apex and base. Internal locule surface smooth or rugulate-striate. Locule uninterrupted.

Follicle wall ca. 0.2 mm thick, thickening at

←  
 ×1.—17. Specimen in Figure 15 rotated through approximately 90°, showing lateral views of numerous curved follicles, and position of fracture surface in Figure 18 (B–B); ×1.—18. PMNH 2403-5 seen from above, showing the position of various fragments and the section, A–A. The exposed fracture surface shows a collar formed by the laminae of persistent flaps attached immediately below the gynoecial zone (line B–B in Figs. 17, 24); ×1.—19. Specimen in Figure 17 rotated through approximately 45°, showing numerous curved follicles radiating from the receptacle; ×1.—20. PMNH 2405, fracture surface B–B (Figs. 17, 18, 22) seen obliquely from above showing the cylindrical portion of the receptacle with the bases of numerous helically arranged flaps, the upper flaps form the prominent, persistent, overlapping flaps of the collar, as seen in face view in Figure 18; ×1.—21. Surface detail of flap laminae showing a granular texture finer than that of the sandstone matrix, ×2.5.—22. Specimen in Figure 20 rotated through approximately 45°, showing a lateral view of the surface of section A–A, the curved cylindrical portion of the receptacle and the position of fracture plane B–B; ×1.—23. PMNH 2405, same specimen as Figure 22 showing the base of the receptacle from above, note the differential penetration of sediment into the receptacle base which shows three zones: a central core interpreted as pith, a ring of discrete wedges interpreted as xylem, and an outer zone interpreted as cortex; ×1.—24. PMNH 2404, counterpart of Figure 22, showing a lateral view of the surface of section A–A, the curved cylindrical portion of the receptacle and the position of the fracture plane B–B; ×1.





FIGURES 25-32. *Lesqueria elocata* Crane & Dilcher, comb. nov., IU 15726-4419, Woodbine Formation, Denton County, northeast Texas.—25. Lateral view showing abraded outer surface;  $\times 1$ .—26. Specimen seen from below showing radiating follicles and receptacle cavity, note the remains of the flaps (F) between the follicles and the cylindrical portion of receptacle: A-A line of fracture surface;  $\times 1$ .—27. Fracture of specimen along line A-A (Fig. 26), showing the cavity formed by the swollen gynoeceal zone of the receptacle, radiating follicles, and the upper part of the cylindrical portion of the receptacle;  $\times 1$ .—28. Counterpart of fracture plane in Figure 27;  $\times 1$ .—29. Latex rubber cast showing the ovoid gynoeceal zone of the receptacle and the bases of numerous helically arranged follicles;  $\times 1$ .—30. Detail of Figure 28 showing the bases of the upper flaps borne on the



the distal end. Seeds 10–20, borne in 2 rows along either side of the median line, slanted adaxially to abaxially, proximal to distal, 3 mm long, 1.5 mm wide.

DISCUSSION: None of the specimens have plant tissues preserved, either organically, or in mineralized form, and all of the details reported in the diagnosis and description are preserved as cavities or impressions in the encasing sandstone matrix. In places, particularly in IU 15726-4419, there is a fine-grained ferruginous sheath surrounding the cavities left by the plant tissue, similar to that reported by Spicer (1977) for Dakota Sandstone leaf fossils and leaves from Recent depositional environments. None of the impressions, however, have yielded cellular detail. Although there has been some distortion, none of the specimens were significantly compressed during fossilization.

Only UKDSC 203 shows the way in which the flowers were borne on the vegetative axis (Figs. 3, 8). At the apex of this vegetative axis there are the bases, or positions of attachment of four other floral receptacles in addition to the one more or less complete fruit (Figs. 7, 8). One of these receptacle bases is 12 mm long and clearly shows the attachment of the proximal flaps to the receptacle. The others are 4 mm long or less and abruptly truncated, suggesting that the fruits frequently abscised at the receptacle base when mature. PMNH 2405 clearly became detached at this point (Figs. 22–24), and the manner in which the sediment differentially penetrated the base of the receptacle (Fig. 23) has provided some information on the anatomical structure at the base of the flower (Fig. 42D).

In addition to the receptacles or receptacle attachments, on UKDSC 203 there are three other projections into the matrix from the apex of the vegetative axis. They are smooth walled, taper distally, and are all less than 10 mm long. They may have been formed by buds, or in the case of the smallest, perhaps by a petiole base. At least one of these holes seems to subtend a floral axis, but the others do not clearly show a similar relationship.

The complete proximal cylindrical zone of the

receptacle is preserved in UKDSC 203 (Figs. 2, 3), PMNH 2405 (Figs. 20, 22, 24), and USNM 2782, 50598 but the distal gynoecial zone is most complete in IU 15726-4419 (Figs. 27, 28). The two specimens from Texas show slight differences from the Kansas specimens, for example IU 15726-4419 has straighter follicles, and the very short cylindrical portion of the receptacle preserved in USNM 326817 shows no sign of laminar flaps. However, the evidence to separate these two specimens is weak and we include them with the Kansas material of *L. elocata*.

The gynoecial zone of IU 15726-4419 is slightly compressed laterally from what we assume was originally a symmetrical rounded cone but merges gradually at the base with the zone below (Figs. 27, 28, 30). In UKDSC 203 and USNM 50598 the transition into the cylindrical portion of the receptacle is more abrupt (Figs. 2, 3).

The cylindrical portion of the receptacle is probably equivalent to the "cylindrical scaly pedicel" mentioned by Lesquereux (1892). The bases of these flaps, which produce the characteristic diamond-shaped pattern on the receptacle, change in size and shape from the apex to the base (Figs. 7, 22), but the transition is gradual. In UKDSC 203 the receptacle is interrupted approximately in the middle of this zone and was blocked by a small plug of sandstone that must have penetrated through a line of weakness in the rotting receptacle relatively early in fossilization (Fig. 7).

The impressions formed in the matrix by the flaps gradually become thinner away from their attachment, and there is no indication of a regular abscission layer (Fig. 7). We imagine that the flaps were persistent and rotted or withered while still attached to the receptacle. A few of the flaps on PMNH 2405 show a weak adaxial keel at their base. Their morphology is otherwise unclear and they show no sign either of pollen sacs or venation (Figs. 18, 21, 42B, C). We do not know their original size or shape, but certainly those immediately below the flower were substantial and formed a prominent collar around the base of the gynoecium (Figs. 18, 20, 22, 42A). The largest collar of persistent flaps is seen in

receptacle immediately below the follicles;  $\times 3$ .—31. Detail of Figure 28 showing longitudinal fracture through three follicles. Note locule casts (K), very short constrictions forming the stalk (L) and the expanded follicle bases (M);  $\times 6$ .—32. Detail of Figure 27 showing molds of expanded follicle bases;  $\times 4$ .



PMNH 2405, but smaller flaps occur in USNM 50598, IU 15726-4419 (Fig. 26), and UKDSC 203 (Fig. 7). A specimen figured by Lesquereux (1892, pl. 2, fig. 9a) may be the base of the gynoecial zone, and its collar of persistent flaps, seen from below.

The transition that the bases of the flaps exhibit along the receptacle could reflect a gradual change in the size and shape of the lamina. Two interpretations seem possible to us: either there was a gradual transition between two kinds of perianth parts, or a transition from stamens with broad laminar filaments to tepals. We have no data to favor one explanation over the other and have seen no evidence of pollen sacs on the upper flaps. A bisexual flower would be more consistent with our interpretation of the systematic affinities of *Lesqueria* based on the number and arrangement of the carpels. Unisexuality is relatively uncommon among living plants with polycarpic flowers, but this possibility cannot be excluded.

The expanded bases of the follicles, the short stalks, and their attachment to the receptacle are best seen in IU 15726-4419, which clearly shows them arranged in helices (Figs. 27, 28, 31, 32). The follicle bases are similar in PMNH 2405 but less well preserved. Other details of the follicles are well preserved in UKDSC 203 (Figs. 4-6, 9) although the apices are also seen in USNM 2782, 50598, 326817, FM-P3056 (Fig. 16), and PMNH 2405 (Figs. 15, 17). These specimens show narrow bilobed terminal prolongations of the follicles that probably correspond to the 'bristles' mentioned and figured by Lesquereux (1892, pl. 2, fig. 9). In a few follicles the extreme apex of each style-like prolongation is slightly expanded, and it is possible that this swelling, and perhaps also the adaxial crest, may have been stigmatic. The two style-like prolongations occur in both dehiscent and non-dehiscent follicles so we discount the idea that they are formed by splitting of a single elongated style at maturity.

In dehiscent follicles the matrix penetrated through the open adaxial suture and also distally between the two apical prolongations (Fig. 9). Where a complete cast of the locule is formed in this way, both internal and external features of the follicle and the thickness of the follicle wall can be interpreted (Fig. 9). Two follicles on UKDSC 203 show irregular holes in the locule fill arranged in a single line on either side of the median plane (Figs. 10, 42G). They are slanted from proximal to distal, adaxially to abaxially,

and we interpret these as molds of seeds. We estimate there would have been approximately ten to 20 seeds in each follicle. In his original description of the species Lesquereux (1892) mentioned transverse undulations in some follicles that may also reflect the positions of seeds. In USNM 326817, the cast of the inner locule surface shows a distinctive rugulate-striate pattern oriented proximally to distally, adaxially to abaxially, but in all other specimens the locule surface is smooth. Reconstructions of the *Lesqueria* follicles are given in Figure 42E-G.

In his discussion of *W. hespera* Wieland (1928: 46) mentioned "three scale-like bodies about each sporophyll or unit." Each of these sporophylls is equivalent to what we interpret as follicles. We have seen no good evidence of any organs at the base of each follicle but the cavities that Wieland interpreted as 'scale-like bodies' are visible on FM-P3056, and in his original specimen PMNH 2405 (Figs. 15, 16). In our view these cavities are spaces remaining between the follicles that were not filled by either sand or mineral deposition during fossilization, and they are quite different from the cavities formed as molds around the plant tissues. In places mineralization seems to have followed the plant surfaces but did not completely fill the cavities between them, particularly where no sand had penetrated. Similar cavities occur occasionally between the two terminal prolongations of the follicles, an unlikely position for scales. Where they occur, these cavities are irregularly arranged and are completely absent from USNM 2782, 50598, and UKDSC 203.

#### COMPARISON WITH FOSSIL PLANTS

Although the holotype of *Williamsonia elocata* Lesq. is lost, from the original description and illustration we have no hesitation in assigning our specimens to this species and establishing UKDSC 203 from the same geological formation and the same geographical area as a neotype. *Williamsonia hespera* Wieland (1928) and *Isoetites* sp. (Brown, 1958) are clearly the same species. Seward (1917) and Wieland (1928) questioned the assignment of *W. elocata* and *W. hespera* respectively to the genus *Williamsonia*. We confirm their opinions and have no doubt that both species belong neither in *Williamsonia* nor the Bennettitales. The structures at the apex of the receptacle are follicles with a distinct longitudinal adaxial suture and contain seeds. In *Williamsonia* we would expect 'interseminal' scales



among stalked ovules, with bracts ('perianth') below (Harris, 1969). In our view *Lesqueria elocata* is clearly a multifollicular angiosperm fruit.

The reassignment of "*Williamsonia*" *elocata* to the angiosperms calls into question the relationship of other poorly understood Cretaceous *Williamsonia*-like plant organs for example: *Palaeanthus hollickii* Seward & Conway (1935a) from the Upper Cretaceous of Kingitok, West Greenland; *Palaeanthus tenuistriatus* Seward & Conway (1935b) from the Upper Cretaceous of Igdloungvak in the same area; *Palaeanthus* sp. Seward & Edwards (1941) from the Palaeocene of Kangerdlugssuak, East Greenland; *Palaeanthus prindlei* Hollick (1936) from the Palaeocene of Alaska; *Williamsonia cretacea* Heer (1880) from the Upper Cretaceous of Atanikerdluk, West Greenland; *Williamsonia reisii* Hollick (1906; Leppik, 1963) from the Upper Cretaceous of Staten Island; *Williamsonia delawarensis* Berry (1916) from the Upper Cretaceous of Maryland; *Velenovskia opatovicensis* Knobloch (1974) from the Cenomanian of Czechoslovakia; and many other poorly known species that might be interpreted as angiosperms just as easily as bennettitaleans on the data available. We have seen none of the original specimens, but these and similar species would be worth reexamining. We have, however, examined specimens of two *Williamsonia*-like fossils, *Williamsonia? recentior* Dawson and the type species of *Palaeanthus*, *P. problematicus* Newb.

*Williamsonia? recentior* Dawson (1886; Seward, 1917; Bell, 1956) is from the 'Upper Blairmore Flora' of southwestern Alberta, generally accepted as of Albian age (Glaister, 1959; Norris, 1964; Rudkin, 1964; Mellon, 1967; Price & Mountjoy, 1970; Stelk, 1975; Stott, 1975; and Singh, 1975). The holotype of the species (Fig. 37) is preserved as a compression in an indurated grey shale. It shows a head of numerous, apparently helically arranged, follicles with indications of scars below. The follicles show curvature similar to those of *Lesqueria*. We estimate that the gynoeceal zone bore about 150 to 200 follicles. The general appearance of the head (but not of the remainder of the receptacle) is similar to *L. elocata*. The scars and remainder of the receptacle are more similar to *Archaeanthus linnenbergeri* (Dilcher & Crane, 1984).

The original material of *Palaeanthus problematicus* described by Newberry (1886, 1895) is from the Amboy Clays (Raritan Formation) of New Jersey, which are generally regarded as of

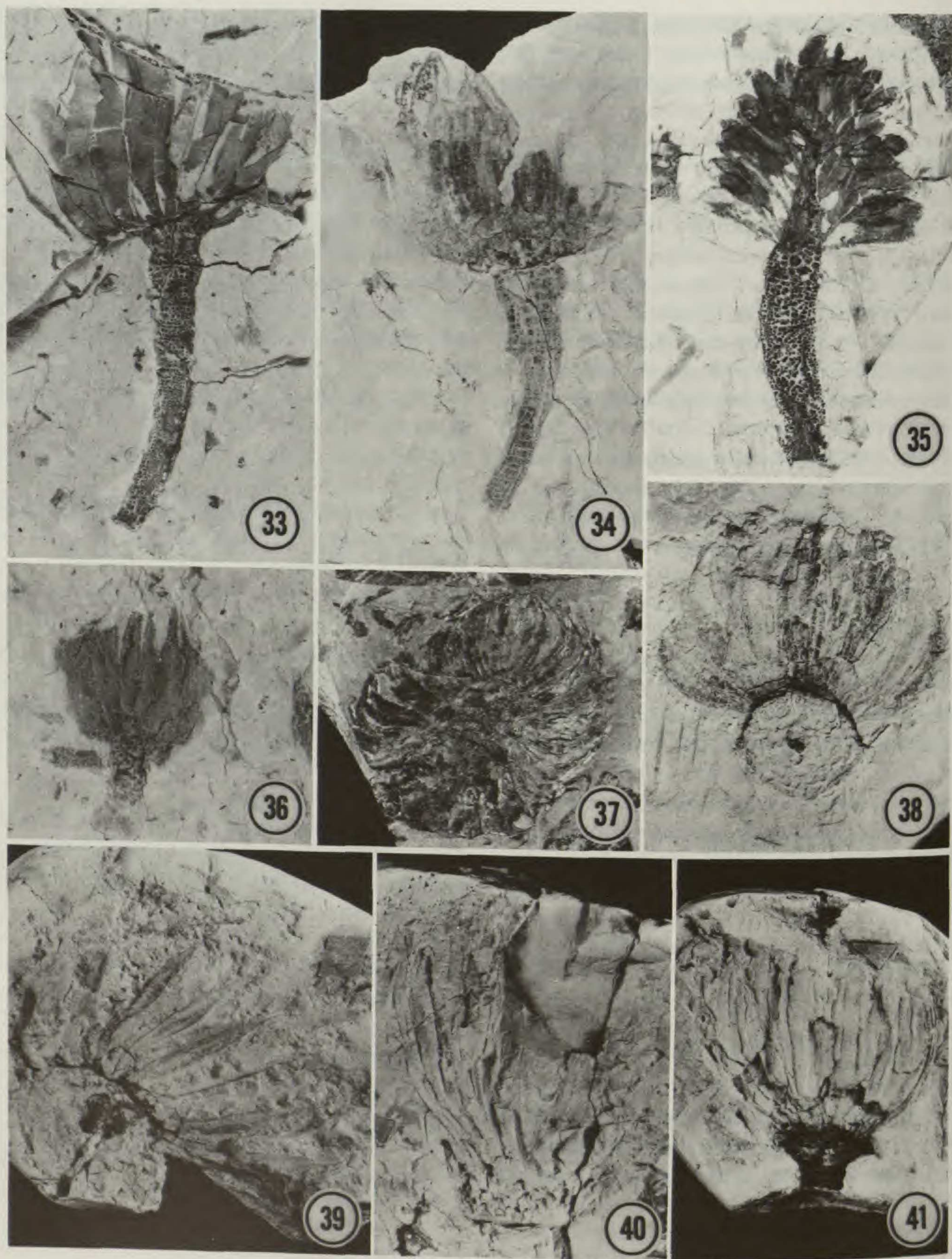
Middle to Upper Cenomanian age (Christopher, 1979 and references cited therein). We have not seen the specimens described later from Gay Head, Martha's Vineyard (Hollick, 1896, 1906) and Glen Cove, Long Island (Hollick, 1912) but from the illustrations judge that they may be a different taxon. The specimens from New Jersey (Figs. 38–41) are preserved in a grey micaceous silty-clay, and although organic material may once have been present, most of it is now missing. However, the impressions show heads of about 50 to 80 follicles, some with a longitudinal adaxial suture; these are surrounded by another zone of more or less linear, to narrowly triangular, structures. Two of the best of these structures on one specimen (New York Botanical Garden, 11420G, now at PMNH) show a prominent bilobed expansion at the apex. Several authors have discussed the botanical relationships of *P. problematicus* (Newberry, 1895; Stebbins, 1940; Cronquist, 1955) and suggestions for closest relatives have ranged from *Williamsonia* to the Compositae. In our view, *P. problematicus* is an angiosperm fruit of many follicles and is very similar to material collected from the Dakota Formation of Hoisington, Barton County, central Kansas (IU 15706) (Figs. 33, 34, 36). One specimen from Hoisington (Fig. 35) is more similar to *Archaeanthus linnenbergeri* (Dilcher & Crane, 1984). *Liriophyllum* leaves, probably belonging to the *Archaeanthus* plant, also occur at the Hoisington locality.

*Palaeanthus problematicus* and "*Williamsonia? recentior*" taken in conjunction with *Lesqueria elocata* and *Archaeanthus linnenbergeri* unambiguously demonstrate the diversity and ubiquity of polycarpic flowers among mid-Cretaceous early angiosperms.

#### COMPARISON WITH RECENT PLANTS

Among Recent angiosperms, *Lesqueria* is most similar to polycarpic taxa, most of which occur in the Magnoliidae. The *Lesqueria* head of follicles most closely resembles those of *Magnelietia* (Magnoliaceae; Canright, 1960) and *Talauma* (Magnoliaceae). *Magnelietia hainanensis* has a tight ovoid cluster of carpels borne on a swollen distal portion of the receptacle. The receptacle in *Himantandra* is similar but much smaller. In *Talauma* (Fig. 46) the cluster of carpels at flowering stage is very similar to the head of follicles in *Lesqueria*. *Annona*, *Dugetia* (Figs. 43, 44) (Annonaceae; Fries, 1931, 1934), and *Schizandra* (Smith, 1947) also show tight clusters of car-





FIGURES 33–41. Mid-Cretaceous angiosperm fruits showing clusters of follicles. 33–36. Unnamed specimens from the Dakota Formation, central Kansas. 37. “*Williamsonia*” *recentior* Dawson from the Blairmore Group (Albian) of Alberta. 38–41. *Palaeanthus problematicus* Newberry from the Amboy Clays (Raritan—middle to late Cenomanian of New Jersey).—33. IU 15706-3078;  $\times 1$ .—34. IU 15706-3077;  $\times 1$ .—35. IU 15706-3084;  $\times 0.5$ .—36. IU 15706-3083;  $\times 1$ .—37. Geological Survey of Canada 5105;  $\times 1$ .—38. New York Botanical Garden (NYBG) *s.n.*;  $\times 1$ .—39. NYBG 11447G, Newberry (1895, pl. 35, fig. 7);  $\times 1$ .—40. NYBG 11420G, Newberry (1895, pl. 35, fig. 6);  $\times 1$ .—41. NYBG *s.n.*, Newberry (1895, pl. 35, fig. 2);  $\times 1$ .



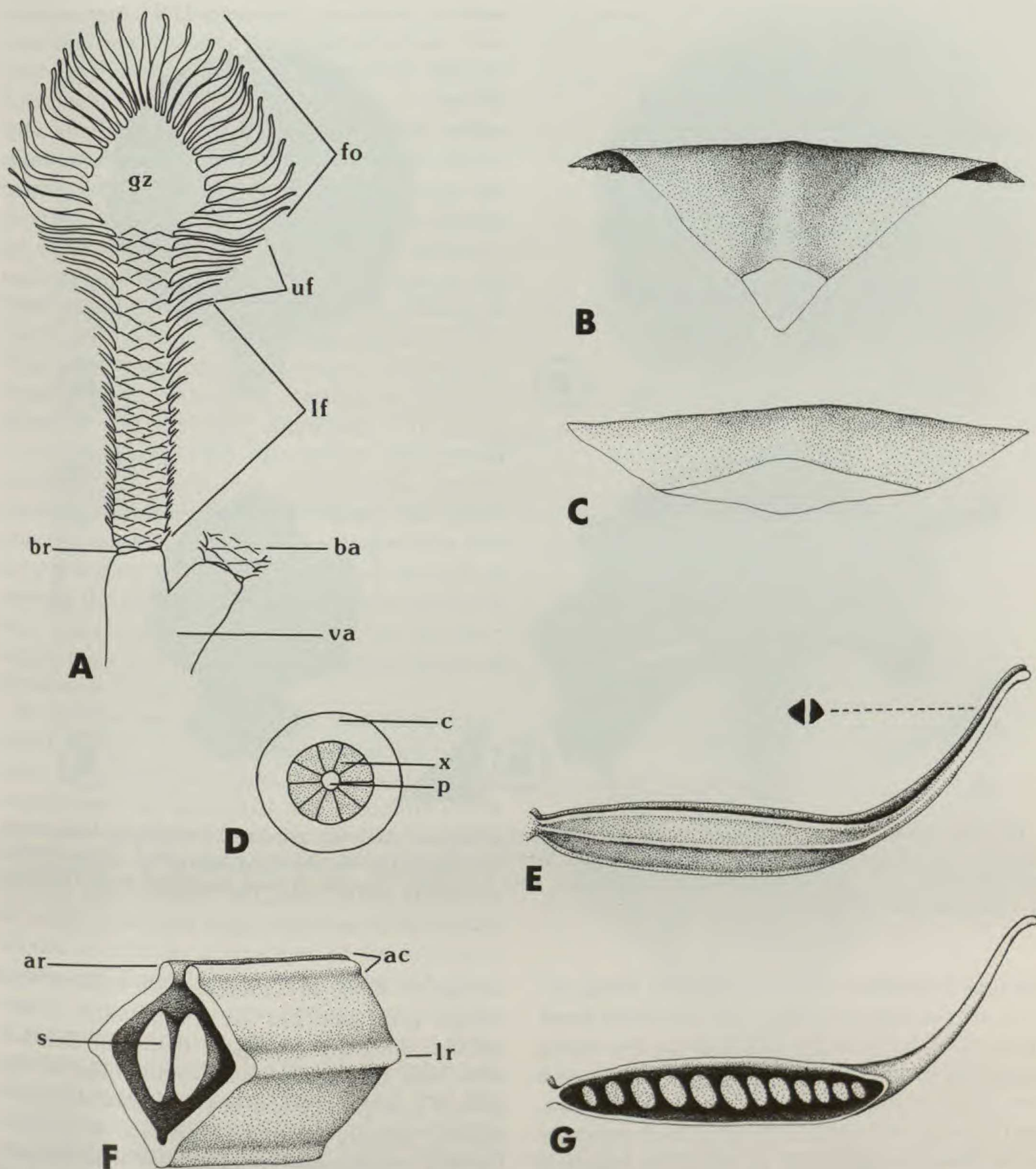
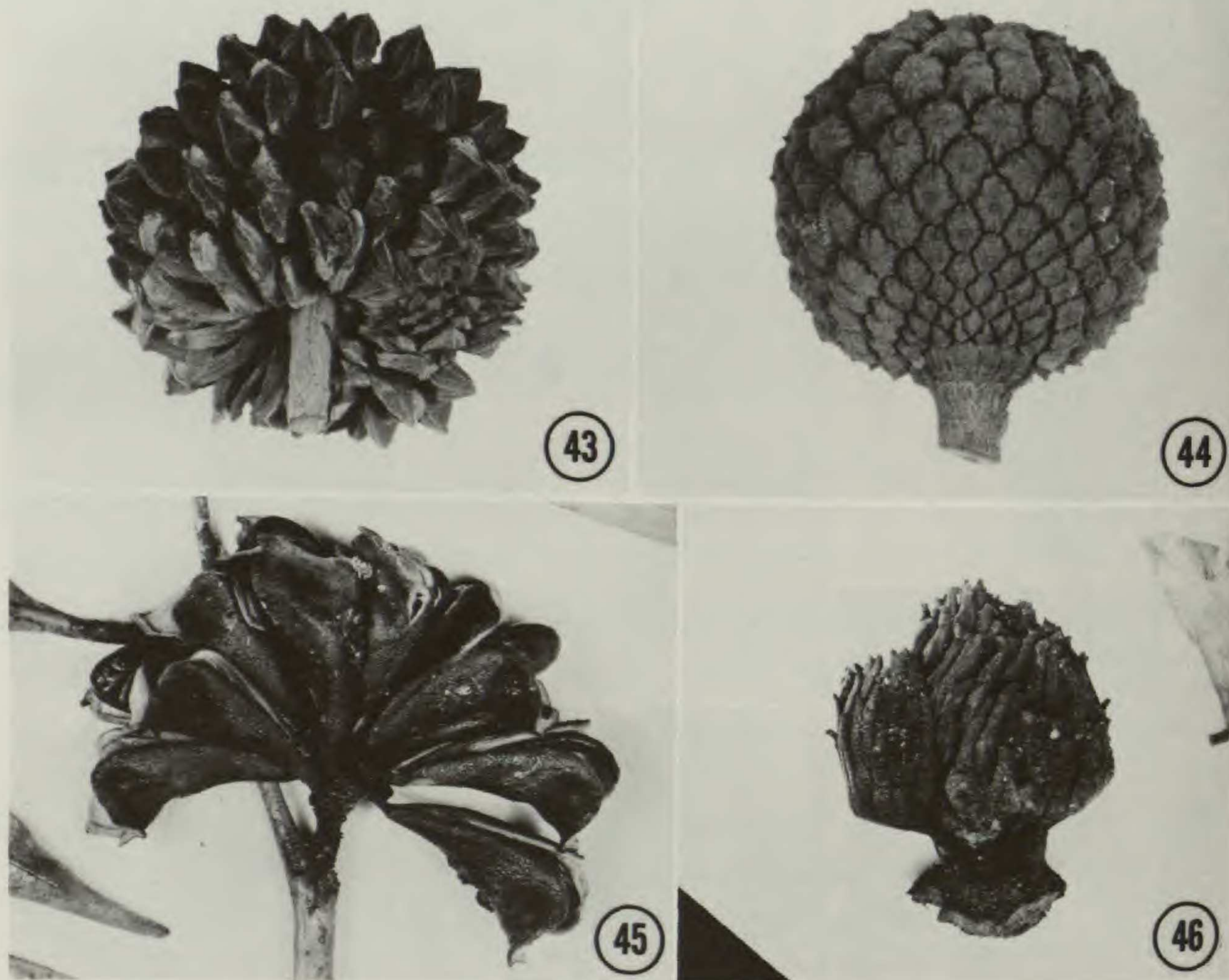


FIGURE 42. *Lesqueria elocata* Crane & Dilchor, comb. nov.—A. Diagram of the *Lesqueria* receptacle and attached organs: fo, tight clusters of follicles; gz, swollen gynoecial zone of the receptacle; uf, upper flaps forming a collar; lf, lower flaps; br, constriction at the base of the receptacle; ba, broken base of another receptacle; va, vegetative axis.—B. Drawing of an upper flap in the collar region removed from the receptacle.—C. Drawing of lower flap removed from the receptacle.—D. Diagram showing the anatomical structure of the receptacle base: c, cortex; x, xylem; p, pith.—E. Reconstruction of a single follicle.—F. Section through follicle: ac, adaxial crest; ar, abaxial ridge; lr, lateral ridge; s, seed.—G. Diagrammatic median longitudinal section of a single follicle showing position of seeds.

pels, but in *Schizandra* the receptacle elongates dramatically at maturity. None of these genera, however, have the gynoecial zone at the apex of a long cylindrical receptacle, such as occurs in

*Lesqueria*. All, however, are bisexual and would be consistent with an interpretation of the persistent upper flaps in *Lesqueria* as stamens. Whatever the botanical nature of these flaps,





FIGURES 43–46. Fruits of Recent plants with numerous follicles. MO, herbarium of the Missouri Botanical Garden.—43. *Dugetia uniflora* (Dun.) Mart., Brazil, MO 2765089;  $\times 1$ .—44. *Dugetia cordata* R. E. Fries, Brazil, MO 2873354;  $\times 1$ .—45. *Anaxagorea* sp., Venezuela, MO 2726969;  $\times 1$ .—46. Young multifollicle of *Talauma* sp., Panama, MO 2778717;  $\times 1$ .

gradual transitions between different floral organs are common in plants with numerous floral parts. Gradual transitions of stamens into tepals occur, for example, in *Eupomatia*, *Paeonia*, and the nymphaeaceous genera *Euryale*, *Nymphaea*, and *Victoria* (Moseley, 1958). However, we know of no Recent angiosperm in which the length of the non-gynoecial portion of the receptacle is as elongated as it is in *Lesqueria*. Another unusual feature is the persistence of the flap-like floral organs below the follicles. Many parallels exist in the Magnoliidae, however, for the clustered arrangement of flowers in *Lesqueria*. The irregular cymose inflorescences of some Annonaceae, for example, are quite similar.

The double follicle tip in *Lesqueria* is similar to the double style of *Austrobaileya* (Endress, 1980) and *Goniothalamus* (Annonaceae). The fruits of these genera are not follicles, however, and the two styles do not persist to fruit maturity.

Although it is clear from this brief review that some Magnoliidae have various features that are

similar to those of *Lesqueria*, we know of no Recent plant that has the combination of numerous, helically arranged, dehiscent follicles with bifid tips borne in a swollen head at the apex of a long receptacle bearing numerous, persistent, spirally arranged, laminar structures. Further comparison of *Lesqueria* with Recent angiosperms is limited by lack of knowledge of other parts of the plant, including wood, leaves, staminate floral parts, and particularly by the uncertainties over the interpretation of the laminar flaps. However, it is clear that *Lesqueria* is a fruit comprised of many follicles and that the *Lesqueria* plant is an extinct angiosperm, probably most closely related to the magnolialean group of the Magnoliidae.

#### CONCLUSIONS—EVOLUTIONARY SIGNIFICANCE

*Lesqueria elocata* contributes significantly to our knowledge of the reproductive diversity of early flowering plants. Along with *Archaeanthus* (Dilcher & Crane, 1984), *Palaeanthus proble-*



*maticus*, and "*Williamsonia*" *recentior*, it demonstrates that the basic floral organization, consisting of numerous, adaxially dehiscent, follicles borne helically on the distal part of a receptacle with another floral organ(s) below, was widespread and common at an early stage in angiosperm evolution. These plants also illustrate the diversity that magnoliid plants had attained some ten to 15 Ma after the first apparently unequivocal angiosperm leaves and pollen appear in the fossil record (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Doyle, 1978; Hughes et al., 1979). Today the Magnoliidae are extremely diverse and heterogeneous, exhibiting various mosaics of primitive and advanced characters (Takhtajan, 1969; Cronquist, 1981). The fossil evidence from *Archaeanthus*, *Lesqueria*, *Palaeanthus problematicus*, "*Williamsonia*" *recentior*, and other material suggests that the Magnoliidae were also diverse during the mid-Cretaceous. Extinction of some of the mid-Cretaceous magnoliid diversity may well account for some of the large morphological gaps that separate the Recent genera and families in this group.

It is important to recognize that these magnoliid flowers occur contemporaneously with other very different kinds of angiosperms, including bisexual, unisexual, and evidently insect and wind pollinated forms (Dilcher, 1979; Vakhrameev & Krassilov, 1979; Retallack & Dilcher, 1981; Dilcher & Crane, 1984). However the mid-Cretaceous magnoliids are of particular interest in relation to concepts of the primitive angiosperm flower. The current, most widely accepted view, based almost entirely on comparative studies of living plants, is that the Magnoliidae, and in particular the Magnoliales, are the most primitive living group, and that the primitive angiosperm flower was of generalized magnoliid construction (Bessey, 1897; Arber & Parkin, 1907; Bessey, 1915; Cronquist, 1968; Takhtajan, 1969; Hutchinson, 1973; Cronquist, 1981). The hypothetical primitive flower is envisaged as radially symmetrical, bisexual, and entomophilous. The receptacle would have been elongated, bearing numerous helically arranged, undifferentiated perianth parts, numerous laminar stamens, and numerous free, conduplicate carpels that dehisced at maturity along an adaxial suture. The carpels would have contained numerous ovules that developed into many large seeds (Takhtajan, 1969). Although no known fossil plant shows precisely this hypothetical combination of characters, *Lesqueria*, *Archaeanthus*, *Palaeanthus problematicus*, and "*William-*



FIGURE 47. Reconstruction of the *Lesqueria elocata* fruiting axis.

*sonia*" *recentior* conclusively establish that some of these allegedly primitive features are also ancient.

#### LITERATURE CITED

- ANDREWS, H. N. 1980. The fossil hunters. Cornell Univ. Press, Ithaca and London.  
 ARBER, E. A. N. & J. PARKIN. 1907. On the origin of angiosperms. *J. Linn. Soc., Bot.* 38: 29–80.  
 BARTSCH, P. 1896. Notes on the Cretaceous flora of western Iowa. *Bull. Lab. Nat. Hist. Iowa State Univ.* 3: 178–182.



- BAXTER, R. W. 1954. The University of Kansas collection of fossil plants. I. The Dakota Sandstone flora. *Trans. Kansas Acad. Sci.* 57: 41-47.
- BELL, W. A. 1956. Lower Cretaceous floras of western Canada. *Mem. Geol. Surv. Branch, Dept. Mines, Canada* 285: 1-331.
- BERRY, E. W. 1912. Contributions to the Mesozoic flora of the Atlantic coastal plain, VII; Texas. *Bull. Torrey Bot. Club* 39: 387-406.
- . 1916. Upper Cretaceous. Maryland Geological Survey.
- . 1917. Contributions to the Mesozoic flora of the Atlantic coastal plain, XII; Arkansas. *Bull. Torrey Bot. Club* 44: 167-190.
- . 1920. Age of the Dakota flora. *Amer. J. Sci., Ser. 4*, 50: 387-390.
- . 1922. The flora of the Woodbine Sand at Arthur's Bluff, Texas. *Profess. Pap. U.S. Geol. Surv.* 129-G: 153-181.
- BESSEY, C. E. 1897. Phylogeny and taxonomy of the angiosperms. *Bot. Gaz. (Crawfordsville)* 24: 145-178.
- . 1915. The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* 2: 109-164.
- BRENNER, G. J. 1963. The spores and pollen of the Potomac Group of Maryland. *Bull. Maryland Dept. Geol. Mines Water Resources* 27: 1-215.
- BROWN, R. W. 1958. New occurrences of the fossil quillworts called *Isoetites*. *J. Washington Acad. Sci.* 48: 358-361.
- CANRIGHT, J. E. 1960. The comparative morphology and relationships of the Magnoliaceae. III. Carpels. *Amer. J. Bot.* 47: 145-155.
- CAPELLINI, J. & O. HEER. 1867. Les phyllites crétacées du Nebraska. *Schweiz. Naturf. Gesellschaft* 22: 1-22.
- CHRISTOPHER, R. A. 1979. *Normapolles* and triporate pollen assemblages from the Raritan and Magothy Formations (Upper Cretaceous) of New Jersey. *Palynology* 3: 73-121.
- CRONQUIST, A. 1955. Phylogeny and taxonomy of the Compositae. *Amer. Midl. Naturalist* 53: 478-511.
- . 1968. *The Evolution and Classification of Flowering Plants*. Houghton Mifflin, Boston.
- . 1981. *An Integrated System of Classification of Flowering Plants*. Columbia Univ. Press, New York.
- DAWSON, J. W. 1886. On the Mesozoic floras of the Rocky Mountain Region of Canada. *Proc. & Trans. Roy. Soc. Canada* 3: 1-22.
- DILCHER, D. L. 1979. Early angiosperm reproduction: an introductory report. *Rev. Palaeobot. Palynol.* 27: 291-328.
- & P. R. CRANE. 1984 [1985]. *Archaeanthus*: an early angiosperm from the western interior of North America. *Ann. Missouri Bot. Gard.* 71: 351-383.
- DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. *J. Arnold Arbor.* 50: 1-35.
- . 1978. Origin of angiosperms. *Annual Rev. Ecol. Syst.* 9: 365-392.
- & L. J. HICKEY. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- & E. I. ROBBINS. 1977. Angiosperm pollen zonation of the continental Cretaceous of the Atlantic coastal plain and its application to deep wells in the Salisbury embayment. *Palynology* 1: 43-78.
- EICHER, D. L. 1975. Foraminifera and biostratigraphy of the Graneros Shale. *J. Paleontol.* 39: 875-909.
- ENDRESS, P. K. 1980. The reproductive structures and systematic position of the Austrobaileyaceae. *Bot. Jahrb. Syst.* 101: 393-433.
- FRANKS, P. C. 1975. The transgressive-regressive sequence of the Cretaceous Cheyenne, Kiowa and Dakota Formations of Kansas. In W. G. E. Caldwell (editor), *The Cretaceous System in the Western Interior of North America*. Special Pap., Geol. Assoc. Canada 13: 469-521.
- FRIES, R. E. 1931. Revision der arten einiger Anonaceen-Gattungen, II. *Acta Horti Berg.* 10: 129-341.
- . 1934. Revision der arten einiger Anonaceen-Gattungen, III. *Acta Horti Berg.* 12: 1-220.
- GLAISTER, R. P. 1959. Lower Cretaceous of southern Alberta and adjoining areas. *Bull. Amer. Assoc. Petrol. Geol.* 43: 590-640.
- GOULD, C. N. 1900a. Some phases of the Dakota Cretaceous in Nebraska. *Amer. J. Sci., Ser. 4*, 9: 429-433.
- . 1900b. The Lower Cretaceous of Kansas. *Amer. Geol.* 25: 10-40.
- . 1901. The Dakota Cretaceous of Kansas and Nebraska. *Trans. Kansas Acad. Sci.* 17: 122-178.
- GRESS, E. M. 1922. An annotated list of fossil plants of the Dakota Formation (Cretaceous) in the collections of the Carnegie Museum, including descriptions of three new species. *Ann. Carnegie Mus.* 13: 274-329.
- HARRIS, T. M. 1969. The Yorkshire Jurassic Flora, III, Bennettiales. British Museum (Natural History), London.
- HATTIN, D. E. 1965. Stratigraphy of the Graneros Shale (Upper Cretaceous) in central Kansas. *Bull. Kansas Univ. Geol. Surv.* 178: 1-83.
- . 1967. Stratigraphic and palaeoecologic significance of macroinvertebrate fossils in the Dakota Formation (Upper Cretaceous) of Kansas. Pp. 570-589 in C. Teichert & E. L. Yochelson (editors), *Essays in Palaeontology and Stratigraphy*. R. C. Moore commemorative volume. Department of Geology, University of Kansas special publication, 2.
- HEDLUND, R. W. 1966. Palynology of the Red Branch Member (Woodbine Formation). *Bull. Oklahoma Geol. Surv.* 112: 1-69.
- HEER, O. 1861. Reply to Dr. Newberry on the age of the Nebraska leaves. *Amer. J. Sci.* 31: 435-440.
- . 1880. Flora Fossilis Arctica, 6, 1:2. Nachträge zur fossilien Flora Gronlands. *Kongl. Svenska Vetensk. Akad. Handl.* 18: 2.
- HICKEY, L. J. & J. A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev. (Lancaster)* 43: 3-104.
- HOLLICK, A. 1896. Martha's Vineyard Cretaceous plants. *Bull. Geol. Soc. Amer.* 7: 12-14.
- . 1906. The Cretaceous flora of southern New



- York and New England. Monogr. U.S. Geol. Surv. 50: 1-129.
- . 1912. Additions to the palaeobotany of the Cretaceous formation on Long Island No. III. Bull. New York Bot. Gard. 8: 154-169.
- . 1936. The Tertiary floras of Alaska. Profess. Pap. U.S. Geol. Surv. 182: 1-36.
- HUGHES, N. F., G. E. DREWERY & J. F. LAING. 1979. Barremian earliest angiosperm pollen. Palaeontology 22: 513-535.
- HUTCHINSON, J. 1973. The Families of Flowering Plants. Clarendon Press, Oxford.
- KAUFFMAN, E. G., W. A. COBBAN & D. L. EICHER. 1976. Albian through lower Coniacian strata biostratigraphy and principal events, western interior United States. Ann. Mus. Hist. Nat. Nice, IV, XXIII: 1-52.
- KNOBLOCH, E. 1974. *Velenovskia* n.g. aus dem Cenoman Mahrens. Čas. Mineral. Geol. 19(2): 171-173.
- KNOWLTON, F. H. 1901. Reports by Professor F. H. Knowlton on fossil plants collected by T. Wayland Vaughan in Lamar County; by G. H. Ragsdale in Cooke County; by T. V. Munson in Rhamney Hill, Denison, Texas. Pp. 314-318 in R. T. Hill, United States Geological Survey 21st Annual Report, 1899-1900, Part 7.
- LEPPIK, E. E. 1963. Fossil evidence of floral evolution. Lloydia 26: 91-115.
- LESQUEREUX, L. 1868. On some Cretaceous fossil plants from Nebraska. Amer. J. Sci. 46: 91-105.
- . 1874. United States Geological Survey of the Territories. Contributions to the fossil flora of the Western Territories. Part I. The Cretaceous Flora. U.S. Department of the Interior Report of the United States Geological Survey of the Territories 6: 1-136.
- . 1878. Remarks on specimens of Cretaceous and Tertiary plants secured by the survey in 1877; with a list of the species hitherto described. In F. V. Hayden (editor), Tenth Annual Report of the United States Geological and Geographical Survey of the Territories.
- . 1883. United States Geological Survey of the Territories. Contributions to the fossil flora of the Western Territories. Part III. The Cretaceous and Tertiary Floras. Department of the Interior Report of the United States Geological Survey of the Territories 8: 2-108.
- . 1892. Flora of the Dakota Group. Monogr. U.S. Geol. Surv. 17: 1-400.
- MACNEAL, D. L. 1958. The flora of the Upper Cretaceous Woodbine Sand in Denton County, Texas. Acad. Nat. Sci. Philadelphia Monogr. 10: 1-152.
- MARCOU, J. 1864. Une reconnaissance géologique au Nebraska. Bull. Soc. Géol. France, Sér. 2, 21: 132-146.
- MEEK, F. B. & F. V. HAYDEN. 1858. Remarks on the Lower Cretaceous beds of Kansas and Nebraska, together with descriptions of some new species of Carboniferous fossils from the valley of the Kansas river. Proc. Acad. Nat. Sci. Philadelphia 10: 256-266.
- MELLON, G. B. 1967. Stratigraphy and petrology of the Lower Cretaceous Blairmore and Mannville Groups, Alberta Foothills and plains. Res. Council Alberta, Geol. Div. Bull. 21: 1-270.
- MOSELEY, M. F. 1958. Morphological studies of the Nymphaeaceae—I. The nature of the stamens. Phytomorphology 8: 1-29.
- NEWBERRY, J. S. 1859. 3. Dr. Newberry's late Explorations in New Mexico—he shows Marcou's so-called Jurassic to be Cretaceous. Amer. J. Sci., Ser. 2, 28: 298-299.
- . 1860a. Notes on the ancient vegetation of North America. Amer. J. Sci. 29: 208-218.
- . 1860b. Note in reply to Mr. Lesquereux. Amer. J. Sci. 30: 273-275.
- . 1868. Notes on the later extinct floras of North America. Amer. J. Sci. 46: 401-407.
- . 1886. The flora of the Amboy Clays. Bull. Torrey Bot. Club 13: 33-37.
- . 1895. The flora of the Amboy Clays: edited by A. Hollick. Monogr. U.S. Geol. Surv. 26: 1-260.
- NORRIS, D. K. 1964. The Lower Cretaceous of the southeastern Canadian Cordillera. Bull. Canad. Petrol. Geol. 12: Field Conference Guide Book Issue 512-535.
- PESSAGNO, E. A. 1969. Upper Cretaceous stratigraphy of the Western Gulf Coast area of Mexico, Texas and Arkansas. Mem. Geol. Soc. Amer. 111: 1-139.
- PLUMMER, N. & J. F. ROMARY. 1942. Stratigraphy of the pre-Greenhorn Cretaceous beds of Kansas. Bull. Kansas Univ. Geol. Surv. 41: 313-348.
- PRICE, R. A. & E. W. MOUNTJOY. 1970. Geological structure of the Canadian Rocky Mountain between Bow and Athabasca Rivers—a progress report. In J. O. Wheeler (editor), Structure of the Southern Canadian Cordillera. Special Pap., Geol. Assoc. Canada 6: 1-166.
- RETALLACK, G. & D. L. DILCHER. 1981. Early angiosperm reproduction: *Prisca reynoldsii* gen. et sp. nov., from mid-Cretaceous coastal deposits, Kansas, U.S.A. Palaeontographica, Abt. B Paläophytol. 179: 103-137.
- RUDKIN, R. A. 1964. Lower Cretaceous. In R. G. McCrossan & R. P. Glaister (editors), Geological History of Western Canada. Alberta Society of Petroleum Geologists.
- SCOTT, R. W. 1970a. Palaeoecology and palaeontology of the Lower Cretaceous Kiowa Formation, Kansas. Univ. Kansas Palaeontol. Contr. Pap. 52: 1-94.
- . 1970b. Stratigraphy and sedimentary environments of Lower Cretaceous rocks, southern Western Interior. Bull. Amer. Assoc. Petrol. Geol. 54: 1225-1244.
- SEWARD, A. C. 1917. Fossil Plants. Volume 3, Pteridospermeae, Cycadofilices, Cordaitales, Cycadophyta. Cambridge Univ. Press, Cambridge.
- & V. M. CONWAY. 1935a. Fossil plants from Kingitok and Kagdlungnak, West Greenland. Meddel. Grønland 93: 1-41.
- & ———. 1935b. Additional Cretaceous plants from western Greenland. Kongl. Svenska Vetensk. Akad. Handl. 15(3): 1-41.
- & W. N. EDWARDS. 1941. Fossil plants from East Greenland. Ann. Mag. Nat. Hist., Ser. 11, 8: 169-176.
- SINGH, C. 1975. Stratigraphic significance of early angiosperm pollen in mid-Cretaceous strata of Alberta. In W. G. E. Caldwell (editor), The Creta-



- ceous System in the Western Interior of North America. Special Pap., Geol. Assoc. Canada 13: 365-367.
- SMITH, A. C. 1947. The families Illiciaceae and Schizandraceae. *Sargentia* 7: 1-224.
- SPICER, R. A. 1977. Predepositional formation of leaf impressions. *Palaeontology* 20: 907-912.
- STEBBINS, G. L. 1940. Additional evidence for a hol-arctic dispersal of flowering plants in the Mesozoic era. Proc. 6th Pacific Sci. Congr. (1939) Berkeley 3: 649-660.
- STELK, C. R. 1975. Basement control of Cretaceous sand sequences in western Canada. In W. G. E. Caldwell (editor), *The Cretaceous System in the Western Interior of North America*. Special Pap., Geol. Assoc. Canada 13: 427-440.
- STEPHENSON, L. W. 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. *Profess. Pap. U.S. Geol. Surv.* 242: 1-226.
- STOTT, D. F. 1975. The Cretaceous system in north-eastern British Columbia. In W. G. E. Caldwell (editor), *The Cretaceous System in the Western Interior of North America*. Special Pap., Geol. Assoc. Canada 13: 441-467.
- TAKHTAJAN, A. 1969. *Flowering Plants, Origin and Dispersal*. Oliver & Boyd, Edinburgh.
- TESTER, A. C. 1931. The Dakota Stage of the type locality. *Iowa Geol. Surv.* 35: 199-332.
- VAKHRAMEEV, V. A. & V. A. KRASSILOV. 1979. Reproductive organs of a shoot of a flowering plant from the Albian of Kazakhstan). *Paleontol. Zurn.* 1979: 121-128.
- WARD, J. V. 1981. Cheyenne and Kiowa angiosperm pollen—a new late Albian record from the southern part of the Western Interior [abstract]. *American Association of Stratigraphic Palynologists, 14th Annual Meeting, Abstracts*.
- WIELAND, G. W. 1928. Certain fossil plants erroneously referred to cycadeoids. *Bot. Gaz. (Crawfordsville)* 86: 32-49.
- WINTON, W. M. 1925. The geology of Denton County. *Texas Univ. Bull.* 2544: 1-86.
- ZELLER, D. E. (editor) 1968. The stratigraphic succession in Kansas. *Bull. Kansas Univ. Geol. Surv.* 189: 1-81.